A Study of the Reproductive Cycle in the California Acmaeidae (Gastropoda)

Part III

by

HARRY K. FRITCHMAN II

(From the Department of Zoology, University of California, Berkeley, California, and the Department of Biology, Boise Junior College, Boise, Idaho)

(Plates 9 to 14)

Subgenus COLLISELLA DALL, 1871

Acmaea pelta ESCHSCHOLTZ, 1833

Ecology: — This species was studied exclusively from the rocky point south of Rockaway Beach, San Mateo County, California (37°30'25" N.; 122°30' W.). The animals are common there, but are not as numerous as Acmaea scutum Eschscholtz, 1833. They seem to be about equally distributed between zone 2 and zone 3, and appear to require macroscopic algae upon which to browse. Acmaea pelta is somewhat more eurytopic than A. scutum and is often found high on the rocks among tufts of Endocladia and on rocks which are quite rough and have considerable barnacle growth on them. Acmaea scutum seems to prefer smoother surfaces and to avoid barnacles. There is also a behavioral difference in that A. scutum seeks moist, shady spots when the tide is out and may migrate onto the under surfaces. Acmaea pelta appears to be less sensitive to desiccation, perhaps due to its increased shell height and reduced aperture and may remain high on the boulder surface in the full heat of the sun.

Collections: — These were begun on September 25, 1949, and continued to April 16, 1952. At the outset and until mid-September, 1950, the sample consisted of about 25 animals. It became apparent that this rate of collecting would eventually deplete the population, and the number was reduced to 10 animals per collection beginning September 26, 1950, and continuing at this rate until the study was completed. A total of 934 animals was studied; 483 males, 422 females, 27 indeterminate, and 2 immature.

Results: — By comparing (Plate 9) the spawning record of Acmaea pelta with that of A. scutum (Fritchman, 1961), it will be seen that there is a striking similarity between the two. Both species were studied over the same period of time and from the same habitat. During this interval A. scutum definitely spawned 12 times and A. pelta 11 times. The spawnings of both were restricted, for the most part, to the fall, winter, and spring months. Despite this, however, there are only three times when the periods of spawning of the species coincide: January 22 to February 5, 1950, March 28 to April 11, 1950, and April 15 to April 28, 1951. In addition to these, there are three other times in which the spawning periods are adjacent in time to one another. Those of A. pelta are October 9 to October 22, 1949; March 12 to March 28, 1950; and September 26 to October 14, 1950. Thus, of the 11 spawnings of A. pelta, six either coincide with or else precede or follow by a maximum of only two weeks corresponding spawnings by the other common limpet in zone 2, A. scutum.

Analysis of Environmental Conditions Coincident with Spawning: —

As explained for Acmaea scutum, only nine spawning periods can be evaluated with reference to tidal and lunar phases, five being associated with full moons (January 22, 1950, March 28, 1950, June 18, 1950, March 18, 1951, and April 15, 1951) and four with new moons (October 9, 1949, February 5, 1950, March 12, 1950, and September 26, 1950). It is thus impossible to assess the role, if any, played by the moon in the spawning of this species. As previously noted with several other limpet populations, the summer months seem to inhibit the reproductive activity of this species, only the minor spawning of June 18 to July 2, 1950, occurring in this period of high temperature. Since A. pelta has been found to spawn at water temperatures ranging from 48.5°F. (January 22 to Feb-

ruary 5, 1950) to 60.0°F. (September 26 to October 14, 1950), or over the entire yearly mean range of the surface water temperatures, it is doubtful that the spawnings are initiated by critical temperature levels. However, temperature levels may, as indicated before, play a role in rate of gonad redevelopment. During the fall and winter of 1949 we again see a retarded development of the gonads of A. pelta. The fall months of 1950 and 1951, both of which were warmer than 1949, each have two spawnings during that period, while 1949 has but one. It may be supposed that the spawning expected for November, 1949, was postponed until January, 1950. If this is assumed, then a general yearly cycle for A. pelta would appear to be as follows: one or two spawnings in the period of January through April, this depending on the mean temperatures of the winter months (if warm, as in 1950-1951 and 1951-1952 then possibly two, one in January and one or two close together in March and April); a reduced reproductive activity from May through August followed by a spawning in late September and October and another about two months later in November. Thus a total of three, or possibly four, spawnings occur throughout the year.

Acmaea limatula moerchii Dall, 1879

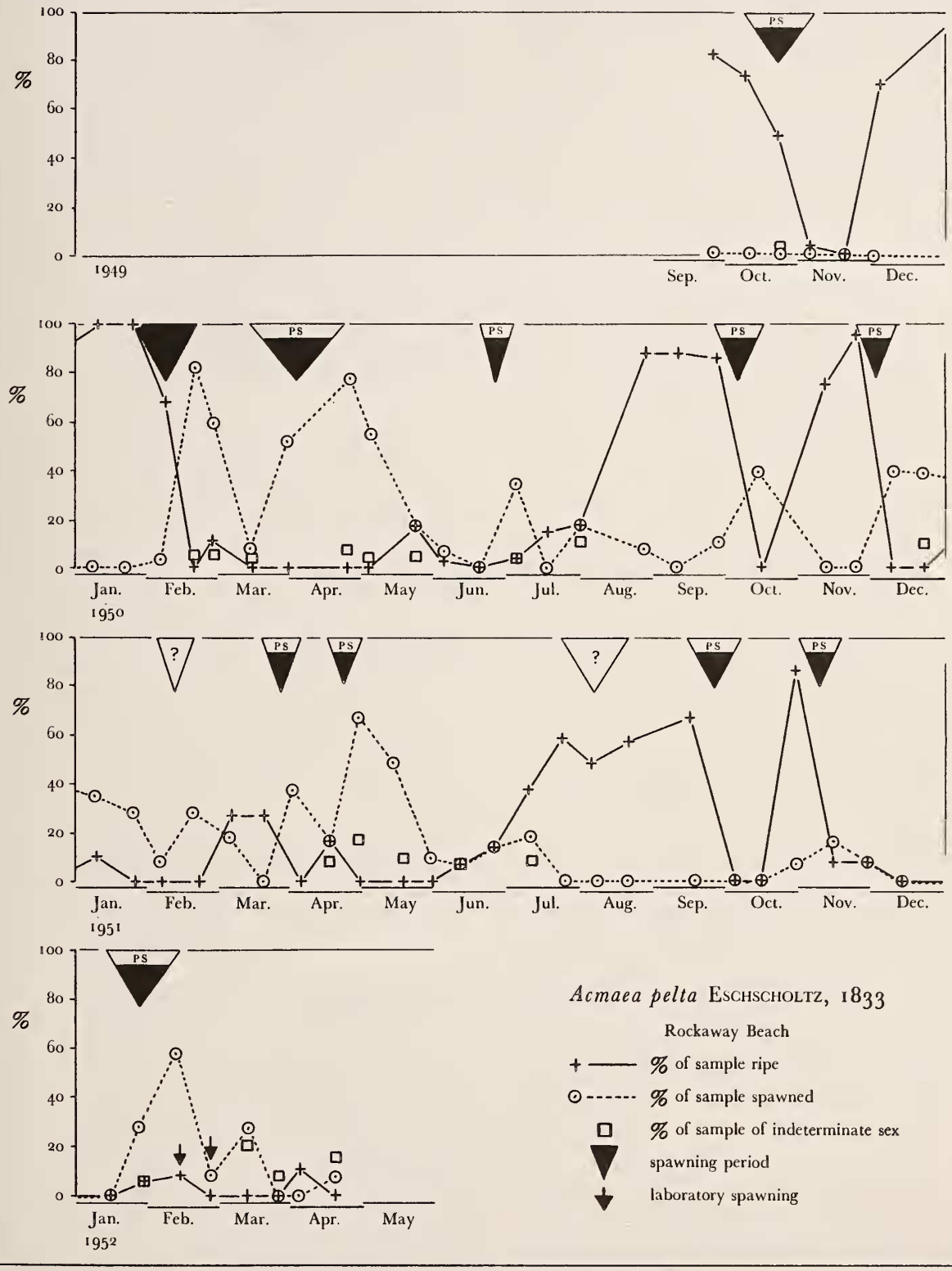
Ecology: — This species does not occur in numbers large enough to be studied north of Monterey, California, except for a restricted population found in Tomales Bay, Marin County, California, where it is the dominant limpet, and because of certain modifications of the shell and its markings, it has been given the rank of a subspecies, Acmaea limatula moerchii Dall. While the open coast A. limatula have a low shell which is predominantly yellow in color and lacking in brown markings, the subspecies moerchii has a high shell similar to that of A. digitalis Eschscholtz, 1833, and is strongly marked with brown. Both the animals from the open coast and bay have the dorsal surface of the foot pigmented with black but the degree of this pigmentation is reduced in the bay form and is rather grayish. In the bay this limpet is very eurytopic and can be found from the upper limit of the barnacle, Balanus, down to the lowest limit uncovered by the tide. The east side of the bay which receives the brunt of the wind and waves from the northwest does not have large growths of algae, probably because of the constant deposition of silt. The only alga present at the sites of collection was small amounts of Ulva, the collections being made at about the level of zone 2. The animals are scrapers of the bare rock surfaces and ingest large amounts of the mud which has settled on them.

Collections: — These were made from three points located at distances of 0.9, 1.5, and 1.9 miles south of the post office of the village of Marshalls (38°09'45" N.; 122°53'30" W.). Collections from the most southern of these areas were begun on October 10, 1950, from the central area on December 31, 1950, and from the northern area on March 25, 1951. Each sample consisted of 10 animals from an area and a total of 434 was examined; 156 males, 204 females, and 74 indeterminate. Collections were made at monthly intervals, the final sample being taken on April 29, 1952. The graph on Plate 10 has been constructed using the information gained from the study of limpets from all three areas, there being little, if any, variation in the reproductive cycles among residents of the three populations.

Results: — It seems apparent (Plate 10) that this species is following a yearly cycle which is different from any encountered thus far in the study. However, the gonad of this species does not develop the extreme turgor which characterizes the ripe condition of many of the other species and for this reason it is difficult to determine when the gonad has progressed beyond the partially ripe stage. These conditions were not included in the plot since the spawned and indeterminate conditions are readily noted and provide a much more dependable basis for establishing the reproductive cycle. The collection of this species began on October 10, 1950, at a time when the animals were just beginning to spawn, as is evidenced by the 40 percent of the first sample which were in the spawned condition. The next collection, made on November 5, showed that approximately 50 percent were indeterminate and it is seen that this condition prevailed until December 31. By late January, 1951, most of the animals were in the process of redevelopment of the gonad, and this condition prevailed until the next spawning season which began in September and reached its peak in October. Here again indeterminate animals appear following the completion of spawning. Acmaea limatula moerchii thus spawns during the time of year when mean sea and air temperatures are at their maxima, a fact that correlates with the southern distribution of the species. The attainment of these temperature levels undoubtedly determines the period of reproduction in this species. Possible stimuli to spawning cannot be speculated upon since collections were made only at monthly intervals.

Acmaea asmi (Middendorff, 1847)

Ecology: — This stenotopic limpet is restricted to the shell of the trochoid gastropod, Tegula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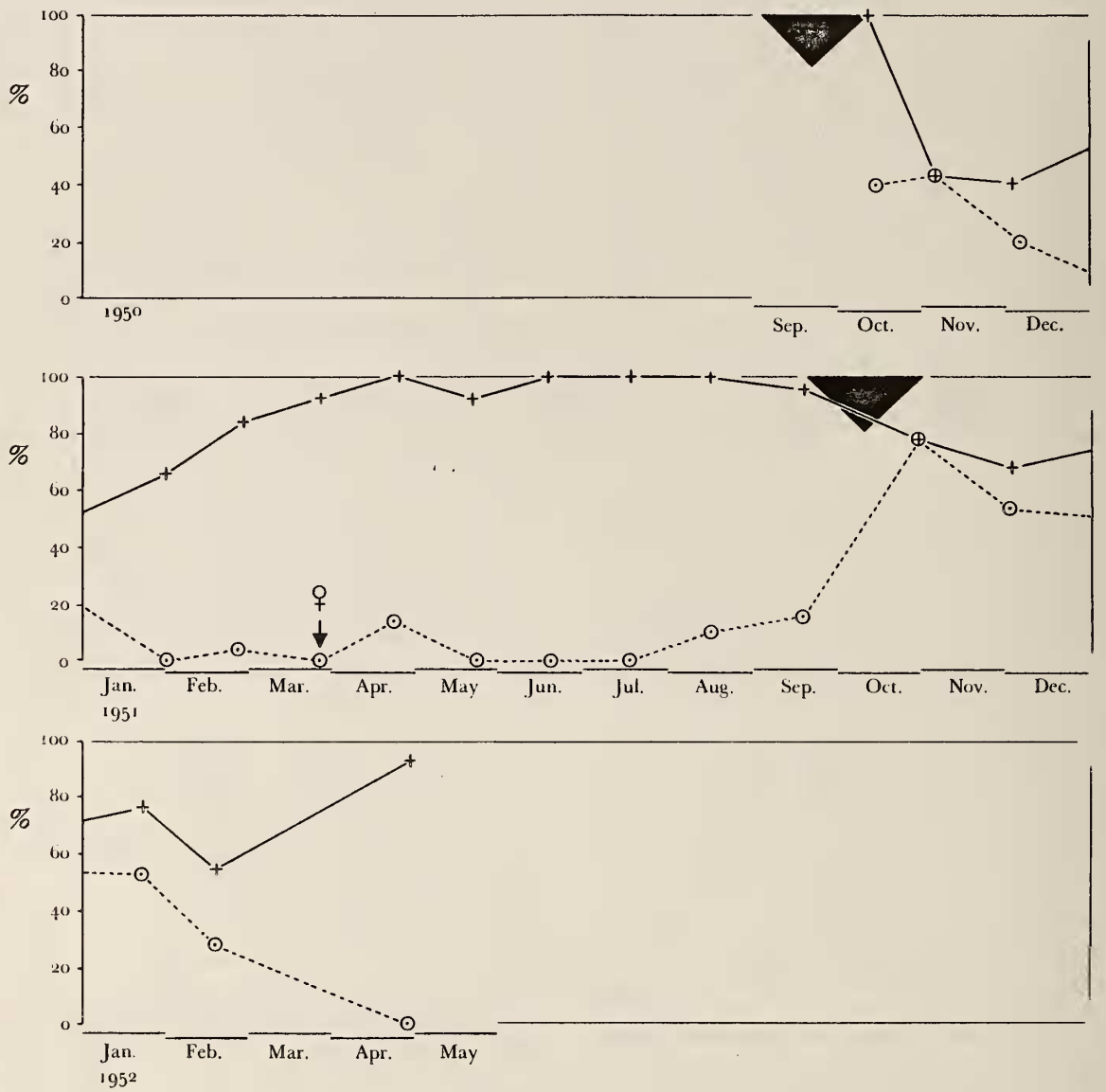
Acmaea pelta ESCHSCHOLTZ, 1833
Rockaway Beach
% of sample ripe
% of sample spawned
% of sample of indeterminate sex
spawning period
laboratory spawning



Acmaea limatula moerchii DALL, 1879

Tomales Bay

+ —— % of sample sexually determinate

⊙ - - - - % of sample spawned

▼ spawning period

↓ laboratory spawning

funebralis (C. B. Adams, 1854), a common zone 2 resident. This small limpet gathers its entire food supply from the diatoms and other microscopic plant life which are present on the Tegula shell. Casual observation of such shells shows that they are singularly barren of vegetable life and are all more or less eroded well into the prismatic layer. If the fecal pellets of the limpet are examined, it will be seen that they are purplish in color due to the large percentage of shell particles which have been rasped from the purple-black host. The poor source of food and the zone 2 location in the intertidal, which restricts feeding time and allows considerable periods of exposure to heating and drying, would appear to combine to render this unique habitat a rather unfavorable one for a limpet, but the species seems quite successful.

Collections: — Acmaea asmi has been collected from a rocky shelf which extends toward the sea and lies just to the north of the mouth of Sunshine Creek, a small stream found at Moss Beach, San Mateo County, California (37°31'30" N.; 122°31'W.). In this area Tegula funebralis is found in abundance, congregated in masses when the tide is out. The procedure was to collect all of the A. asmi present on the Tegula along this shelf at each collecting period. This usually provided between 20-25 animals and, of course, means that the area must be replenished with Acmaea-bearing Tegula every two weeks. Most of the immigrating Tegula probably came from the flat sandstone rocks to the north of the shelf, this area having moderate quantities of various algae growing upon it (Petrocelis, Endocladia, Gigartina, Iridophycus, and Cladophora). Since the creek runs not far to the south, replenishment from that area is unlikely.

Only the adult animals of this species have been examined, and because of the fixed size that the animals can attain, the thickness of the gonad can be used, in combination with that of degree of turgor, as an indication of ripeness. An adult animal which is ripe will have a gonad showing extreme turgor and which will be 1.5 to 2.0 mm. in thickness. Adult animals with gonads of 1.0 mm. or less are considered partially ripe or partially spawned, while spawned animals are readily identified by the thinness of the gonad and the small residual quantities of eggs and sperm. The study of this species was begun on November 5, 1949, and continued until April 16, 1952. However, during the first eight months, considerable difficulty was experienced in identifying the condition of the animals and for this reason these data have been discarded. Plate 11, then, has been prepared from the data of the collections of July 2, 1950, to April 16, 1952. A total of 851 animals was examined; 391 males, 446 females, 12 indeterminate, and 2 immature.

Results: — Acmaea asmi from this area of collection appears (Plate 11) to have a reproductive cycle which includes two spawnings per year, one in the spring in March or April, and another in the fall in September or October. Following the spring spawning, the gonads are redeveloped and remain in a ripe or partially ripe condition during the summer, much as was indicated for A. scutum. However, subsequent to the fall spawning period, this species passes into a rather strange condition, which extends until the following March or April. During this time the gonads are all much as they were at the conclusion of the fall spawning, practically none of them being ripe and a variable percentage spawned, but most of the animals possess gonads of 0.5 to 1.0 mm. in thickness and with moderate amounts of eggs and sperm. This latent period during the winter period is unusual since at that time all of the other species and populations studied are very active reproductively. This spawning pattern, like that found for A. limatula moerchii, reflects A. asmi's southern distribution and greater tolerance for and dependence upon high temperature.

Analysis of Environmental Conditions Coincident with Spawning: —
It is impossible to evaluate the effects, if any, which lunar and tidal periodicity have on this species because of the occurrence of periods of both new and full moons during the interval when spawnings are known to have taken place. As regards temperature, little can be said here since the temperatures at which reproductive activity begins in March and April, 52° to 53° F., is several degrees below that at which it ends, in the cases recorded, 57° to 60°F. It is thus difficult to designate any temperature as a critical one as has been done for several of the other species.

Acmaea digitalis Eschscholtz, 1833

Ecology: — (Rockaway Beach Population)
This species was studied from two localities and these will be considered separately. The first of these is a large concrete breakwater which stands at the tip of the rocky point which forms the southern boundary of the community of Rockaway Beach, California. This structure extends for about 100 feet in a

north-south direction and stands about 12 to 15 feet high. It is anchored in the center to a huge boulder which divides it into north and south portions. It was from the lee side of this north section that extensive collections of Acmaea digitalis were made. The upper surface of the breakwater is never submerged although it is dashed by the surf at high tide. The leeward side furnishes a very uniform environment for the large numbers of A. digitalis which live upon it. The animals are completely protected from the direct beat of the surf and receive their water as it runs down the vertical face of the concrete. They receive uniform illumination from the east and south and are exposed twice daily to desiccation. The only source of food is that of microscopic plant life left by the surf and, during the winter, what algal film can proliferate. Throughout the summer months, the vertical faces appear to be burned bare of any living algae. The only other animals in this habitat consist of a few Littorina scutulata Gould, 1849, L. planaxis Philippi, 1847, and small barnacles, probably Balanus glandula Darwin, 1854. During the summer this habitat undergoes extreme heating and drying during the occasional long periods of low tide. Collections made at such times find the limpets in a state of extreme desiccation, the bodies of the animals being shrunken and brown within their shells, the foot being held to the substrate only by a thin film of dried mucus. This degree of desiccation is caused, to an extent, by the vertical surfaces of the breakwater which almost immediately drain and dry when the last wave of the descending tide has passed over the structure.

Collections: — These were begun from this habitat in February, 1949, and continued to April 16, 1952. A total of 9'902 animals was collected during this period at intervals of two weeks; 3'415 males, 3'365 females, 3'084 indeterminate, and 38 immature. The size of the samples varied. Initially, the sample consisted of approximately 250 animals. This practice was continued until February, 1950, at which time the number was reduced to about 100 per sample. A final reduction was made in October, 1951, to 50 animals per collection.

Results: — Two gonad conditions have been plotted (Plate 12): percent of the sample which was ripe and percent of the sample which was of a determinate sex. The two features which appear most evident from the plot of the reproductive cycle of this population are the single major spawning which occurs during the late winter or spring months and the indeterminate condition which is present during the summer months. The major spawning depletes the gonads completely except for a few residual eggs and sperm masses which remain for one to several months and permit the sex of the animal to be ascertained. Sooner or later these genital products are resorbed and the gonad becomes indeterminate. The major spawning may be preceded by a partial spawning in which all or only part of the animals participate. Such spawnings occurred in mid-January of 1951 and between late February and early March, 1951. After such spawnings, the gonad redevelops to a ripe condition prior to the major spawning. During the winter months when the gonads are developing, indeed, even before they have attained a fully ripe condition, spontaneous spawnings occur in the storage jars in the laboratory. Such occurred eight times during the winter of 1950-1951 and five times during the winter of 1951-1952. Accurate analysis of the condition of the population is seriously interfered with by this type of spawning and one of two alternatives may be used to express the data. One can assume that the population was either ripe or was approaching that condition and plot the sample as being ripe. This practice was followed for the 1950-1951 data. Or one can plot the actual condition of the sample when it was examined regardless of the degree of spawning which had taken place as was done in 1951-1952. The former method is preferred when the population is known to have reached a fully ripe condition prior to the first spontaneous spawning. There will usually be a few animals which will not have spawned and will, by the ripe condition of their gonads, give an indication of the status of the population at the time of collection. However, if the development of the gonad has been retarded as it was in the fall of 1951 and spontaneous spawning occurs prior to the fully ripe condition, then it is impossible to estimate what the natural condition of the population is at the time of collection. In such a case it is perhaps preferable to plot the data as it actually appears at the time of examination. This accounts for the low percentages of ripe animals which appear during the first two months of 1952.

Analysis of Environmental Conditions Coincident with Spawning: —

Of the five spawning periods which can be analyzed relative to the influences of lunar and tidal factors, namely April 24 to May 9, 1949, May 9 to May 23, 1949, March 18 to April 1, 1951, April 1 to April 15, 1951, and March 31 to April 16, 1952, three are associated with full moons and two with new moons. The maximal

tidal ranges of these periods are 6.1, 8.0, 6.5, 5.8, and 6.5 feet. The only spawning period which was accurately reduced to an interval of seven days was that of February 5 to 12, 1950. This was a complete spawning so there could be no possibility of misinterpretation when the animals were examined. Here the tidal fluctuations were only moderate beginning with 5.8 on February 5 and continuing as follows: 5.0, 4.5, 5.0, 5.5, 6.0, 6.5, and 6.8 feet on February 12. Furthermore, this period does not fall under the influence of either a full or a new moon. Thus, there is no reason to suppose that the spawning periods of this population of high intertidal limpets are correlated with lunar periodicity and the attendant high tides. The surface water temperatures at which spawnings occurred are as follows: 1949, 55.0°F.; 1950, 49.5°F.; partial spawning 1951, 50.5°F.; complete spawning 1951, 52.0°F.; partial spawning 1952, 53.0°F.; and complete spawning 1952, 53.5°F.

Acmaea digitalis Eschscholtz, 1833

Ecology: — (Moss Beach Population) There are to be found at Moss Beach, San Mateo County, California, a series of large stone ledges located about 100 yards north of Sunshine Creek. These rocks are from eight to ten feet high and are very soft sandstone. They are seldom completely submerged but are wetted daily by the wash of the tide. The broad horizontal surfaces of the tops of these rocks have several small tide pools which support heavy growths of coralline algae. The top three or four feet of the vertical sides of the rocks support large colonies of limpets. Many occur in small depressions in the rock, either singly or in clusters of several per depression. Of these limpets, Acmaea digitalis is the most abundant, but A. scabra is also very common. The rock at this height supports a moderate growth of green algae, Ulva being the predominant type. In addition to the macroscopic algae, there is a film of microscopic plant life covering the rock. The porous rock allows these plants to thrive at a height which would be impossible, were the rock more dense, since the substrate is always damp. The limpets in feeding scrape up large amounts of sand and with it the attached plant life. Food is plentiful and, in addition, desiccation is reduced by the nature of the rock. All of the limpets were collected from the northern side of the northernmost of these rocks, thus assuring that they were taken from the most favorable area of this habitat which, because of its continued dampness, corresponds roughly to lower zone 2 or upper zone 3.

Collections: — These were begun in February, 1951, and extended to April, 1952. They were made every two weeks, each sample consisting of 15 animals. A total of 416 was examined; 247 males, 156 females, 5 indeterminate, and 8 parasitized.

Results: — The most striking difference (Plate 13) between the reproductive cycles of this population and that of the breakwater is the lack of an indeterminate period during the summer. Of the 416 examined, only five were indeterminate because of a complete spawning. Eight others were found to be indeterminate due to heavy infestations of trematode sporocysts and cercariae. The analysis of this population was more difficult because of its tendency to spawn during storage. This fact itself indicates the increased reproductive potential of this population as compared with that of the less favorable breakwater. These spontaneous spawnings took place throughout the year and resulted in normal trochophore larvae. The best indication of what was taking place in the population in its natural habitat was gained by recording the intensity of the laboratory spawnings and awaiting a sample which did not spawn and which, upon examination, showed itself to consist of recently spawned animals. Plate 13 indicates the condition of the sample when examined and also the extent of the laboratory spawning. By correlating these two pieces of information, the times of natural spawning may be approximated. An example of the method used is seen in relation to the collections of April 1 and April 15, 1951. The first of these spawned heavily as is indicated by the designation +3. This sample is believed to have been ripe when collected. The other sample showed only one ripe animal, the entire group being either completely or partially spawned. It is thus presumed that the population spawned between these dates. On the basis of this type of analysis, it is believed that the population spawned three times during 1951. This is considered, however, to be a conservative estimate. When the spawning reaction is as easily provoked as it is in this population, it is not at all improbable that minor, undetected spawnings may occur frequently and serve to augment the major spawnings.

The study of this population dramatically illustrates the effect which extrinsic environmental factors can have upon the reproductive capacity of these limpets. Both the Moss Beach and the Rockaway Breakwater populations are unquestionably Acmaea digitalis and in both habitats the limpets are abundant. The difference wrought in these animals by the environment is alteration of the reproductive potential